# Principal component and PLS discriminant analyses applied on skulls of European shrews of the genus Sorex (Mammalia, Soricidae) 

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#### Abstract

Skulls of nine species of shrews of the genus Sorex were measured on an image analyzer. 120 measurements were taken on each skull. The measurements were then statistically analysed by using the multivariate projection methods principal component analysis (PCA) and PLS discriminant analysis combined with crossvalidation. The analyses showed good separation between all species. It was discussed whether this class separation reflected the phylogeny or different ecological adaptations. Key words. Shrews, skulls, phylogeny, principal component analysis, PLS discriminant analysis.


## Introduction

At least thirteen species of the genus Sorex occur in the western Palaearctic except for North Africa and most of the Middle East. The species concerned are S. alpinus, S. araneus, S. caecutiens, S. caucasicus*), S. coronatus, S. granarius, S. isodon, S. minutissimus, S. minutus, S. raddei, S. samniticus, S. "tundrensis" (the status of the Eurasian animals earlier placed in S. arcticus is still not clear, Kozlovsky 1971 found S. irkutensis and S. sibiriensis to be distinct karyotypically) and S. volnuchini. Two additional species, S. daphaenodon and S. vir (probably identical with S. roboratus of the Altai, see Hoffmann 1985) occur in Siberia almost west to the Ural mountains, but are not yet known from Europe.

The distributions of the fifteen species named above are chiefly of two different types. Many species have large west-east distributions chiefly in the taiga zone of Eurasia though some (e. g. S. araneus and S. minutus) also occur south of the coniferous forest-zone. Of these species $S$. araneus and $S$. minutus might be regarded as mainly European. They occur over large areas in Europe but in Asia they only reach eastward to the Yenisei River and Lake Baikal, while S. caecutiens, S. daphaenodon, S. isodon, S. minutissimus, S. "tundrensis" and $S$. vir all might be regarded as mainly Asian; their European distribution is (if they occur at all) limited while in Siberia they all reach eastward to the Pacific Ocean (Dolgov 1967, Honacki, Kinman \& Koeppl 1982).

Another type of distribution is shown by Sorex-species occurring in rather limited, chiefly mountainous areas in southern Europe. Such forms occur in Spain ( $S$. granarius) and in the Caucasus (S. caucasicus, S. raddei and S. volnuchini). S. alpinus

[^0]is spread over a large area in south and central Europe but again chiefly at higher altitudes while S. samniticus occurs in lowlands in Italy. All these distributions might be regarded as relic distributions.

The only species not showing either a continuous west-east distribution in the north or a relic distribution in the south is $S$. coronatus in southwestern Europe. This form probably linked off from $S$. araneus-like forms during the last glaciations.

The relationships of these species are not completely clear. $S$. araneus, $S$. caucasicus, S. coronatus, S. daphaenodon, S. granarius and S. tundrensis together with $S$. arcticus of North America and $S$. asper of the Tien-Shan (Ivanitskaya et al. 1986) form the $S$. araneus/arcticus-group characterized karyologically by two-armed x-chromosomes and (in males) two y-chromosomes (Hausser et al. 1985). This group probably represents a monophyletic unit.

Of the other species, $S$. caecutiens, $S$. isodon, S. minutissimus, S. minutus, S. raddei, S. vir and S. volnuchini all have karyotypes with either the chromosomal number of 42 or a chromosomal number close to or possibly derived from 42 (Fedyk \& Ivanitskaya 1972, Ivanitskaya et al. 1986). This group might not be a monophyletic unit; according to Fedyk \& Michalak (1982) the similarity of the number of chromosomes in S. minutus on one hand, and S. isodon, S. vir etc. is fortuitous.

Finally, S. alpinus and S. samniticus have karyotypes very different from the other species and also from each other (Meylan 1964, Graf et al. 1979). These two species appear not to be closely related to any other living Sorex-species; they might be relic forms of two otherwise extinct branches of the genus.

The aim of this paper was to statistically analyse the morphology (chiefly expressed by measurements) of shrew skulls and compare the patterns of relations between different species thus obtained, to those obtained using karyological methods.

Relationships between different species are not necessarily reflected in skull morphology. S. alpinus, the most isolated species karyologically, is certainly also the most isolated in gross morphology, while S. samniticus is morphologically very similar to $S$. araneus, $S$. coronatus and $S$. granarius, which are members of the $S$. araneus/arcticus-group. The morphological and genetic differentiation of the latter four species has been statistically treated by Hausser (1984). A limitation in univariate statistical methods is that each variable is treated separately. This might lead to unwarranted results. "Class differences are not clearly seen in the individual variables. The classes are separated by a combination of the variables" (citation from Wold et al. 1983).

Models like SPSS (used by Hausser) and SIMCA (used here) are, however not "one variable at a time" models. Thus in this work principal component analysis and partial least squares (PLS) discriminant analysis have been used. These methods are multivariate and deal with all variables simultaneously.

## Material and methods

19 skulls each of S. alpinus, S. araneus, S. caecutiens, S. coronatus, S. isodon and S. minutus, 13 of S. granarius and S. samniticus and 7 of S. minutissimus were measured on an image analyser (MOP Videoplan, Kontron image analysis division, Zeiss), connected to a dissecting microscope ( 19 were measured because there were 19 channels in each file on the image analyser). The animals were obtained from the Swedish Museum of Natural History,


Fig.1: Cranial measurements taken for this study. Explanations of figures are given in the text.

Stockholm, from the University of Oulu, Finland and from the Université de Lausanne, Switzerland. The geographical origin of the animals is given in Table 1. Other species mentioned in the introduction were not available to me.

From each individual 120 measurements were taken (see Figs 1-2). Most of them were metrical measurements, but some characters such as the position of the mental and lacrimal foramina, size and pigmentation of cusps of upper molars, or the angle between the coronoid process and the articular facets of the mandibular condyle.

These characters were treated in the following way. Taking the position of the mental foramen as an example this character was given the value 1 if the foramen was placed under $P_{4}$ the value 2 if it was under $\mathrm{P}_{4}-\mathrm{M}_{1}$, the value 3 if it was situated under the foremost part of the trigonid of $M_{1}$, the value 4 if it was placed centrally under the trigonid of $M_{1}$ and so on, up to the value 8 . Another example can be given like size and pigmentation on the
hypocone of $\mathrm{M}^{1}$. In this case the character was given the value 1 if the hypocone was absent, the value 2 if it was rudimentary, the value 3 if it was distinct but unpigmented and the value 4 if it was distinct and pigmented.


Fig. 2: Mandibular measurements taken for this study. Explanations of figures are given in the text.

Table 1: Number of skulls of each species.

| Species | Number <br> of skulls | Geographical area | Source |
| :--- | :---: | :--- | :---: |
| Sorex alpinus | 19 | Switzerland, Germany, Yugoslavia | 1,3 |
| Sorex araneus | 19 | Sweden, Finland, Germany, Czechoslovakia | 1 |
| Sorex caecutiens | 19 | Sweden, Finland | 1,2 |
| Sorex coronatus | 19 | Switzerland | 3 |
| Sorex granarius | 13 | Spain | 3 |
| Sorex isodon | 19 | Finland | 2 |
| Sorex minutissimus | 7 | Finland | 2 |
| Sorex minutus | 19 | Sweden, Germany | 1 |
| Sorex samniticus | 13 | Italy | 3 |

Source: $\quad 1=$ Swedish Museum of Natural History, Stockholm, Sweden
$2=$ University of Oulu, Finland
3 = Université de Lausanne, Switzerland

Most measurements were taken on both the left and the right side of the skull which accounts for the high number of measurements. The characters measured are given below, characters given as values are in parentheses.
A. On the skull.

1. Condylobasal length.
2. Breadth of rostrum taken over upper incisors.
3. Maxillary breadth.
4. Interorbital breadth.
(5. Occurrence and size of medial tines on upper incisors.)
5. Cranial height.

The following measurements ( $7-17$ ) taken on the left side.
7. Length of the first cusp of the upper incisor.
8. Length of the second cusp of the upper incisor.
9. Total length of the upper antemolars.
10. Total length of the upper molariform teeth.
11. -15 . Length of $A^{1}-A^{5}$ respectively.
16. Breadth of the zygomatic plate.
(17. Position of the lacrimal foramen.)
18. $-28 .=7 .-17$. from the right side.
29. Cranial breadth.
30. Width of $\mathrm{M}^{2}-\mathrm{M}^{2}$.
31. Palatal length.
32. Glenoid width.

Measurements 33-46 taken of left side.
33. Buccal length of $\mathrm{P}^{4}$.
34. Width of $\mathrm{P}^{4}$.
35. Buccal length of $\mathrm{M}^{1}$.
36. Posterior width of $\mathrm{M}^{1}$.
37. Buccal length of $\mathrm{M}^{2}$.
38. Posterior width of $\mathrm{M}^{2}$.
39. Length of $\mathrm{M}^{3}$.
40. Width of $\mathrm{M}^{3}$.
(41. Size and pigmentation of the protocone on $\mathrm{P}^{4}$.)
(42. - 44. Size and pigmentation of the hypocones on $\mathrm{P}^{4}-\mathrm{M}^{2}$.)
(45. Size and pigmentation of the metacone on $\mathrm{M}^{3}$.)
(46. Size and pigmentation of the protocone on $\mathrm{M}^{3}$.)
47. -60 . $=33 .-46$. from the right side.
B. On the lower jaw ( $61 .-90$. taken on the left lower jaw).
61. Length of the mandible.
62. Height of the coronoid process.
63. Distance between coronoid process and the upper articular facet of the mandibular condyle.
64. Length of the lower incisor.
(65. Number of cuspules on the lower incisor.)
66. Length of mandibular toothrow (except incisor).
67. Length of A1.
(68. Number of cusps on $\mathrm{A}_{1}$.)
69. Length of $\mathrm{P}_{4}$
(70. Position of mental foramen.)
71. Height of the internal temporal fossa.
72. Width of the internal temporal fossa.
73. Length of $\mathrm{M}_{1}$.
74. Trigonid width of $\mathrm{M}_{1}$.
75. Talonid width of $\mathrm{M}_{1}$.
76. Length of $\mathrm{M}_{2}$.
77. Trigonid width of $\mathrm{M}_{2}$.
78. Talonid width of M2.
79. Length of $\mathrm{M}_{3}$.
80. Trigonid width of $\mathrm{M}_{3}$.
81. Talonid width of $\mathrm{M}_{3}$.

Measurements 82. -90. taken on the mandibular condyle.
82. Length of upper condylar facet.
83. Thickness of upper condylar facet.
(84. Angle between coronoid process and upper condylar facet.)
85. The height of the condyle.
86. Greatest condylar depth.
87. Width of interarticular area.
88. Length of lower condylar facet.
89. Thickness of lower condylar facet.
(90. Angle between coronoid process and lower condylar facet.)

Measurements 91. $-120=61 .-90$. from the right side.
The two projection methods principal component analysis (PCA) (Joliffe 1986) and partial least squares (PLS) discriminant analysis combined with cross validation (Ståhle \& Wold 1987, 1988) have been applied.

The PCA can very well be used for recognizing similarities between objects in one class and dissimilarities between objects in different classes and can also be applicated on both continuous and non-continuous variables at the same time (Joliffe 1986).

The PLS discriminant analysis is a new type of discriminant analysis different from linear discriminant analysis (LDA). The PLS approach, which operates on the original variables space, has the advantage that it can deal with highly correlated variables and be applied to problems where the number of variables is high and even exceed the number of observations. The results from PLS can preferably be presented in object and variable related projections with the same interpretation as object and variable related PCA projections.

The calculations have been performed with the SIMCA (Soft Independent Modelling of Class Analogy) pattern recognition package as described by Wold et al. (1983, 1984). Prior to the analysis all variables were scaled variable-wise to zero mean and unit variance. The results were presented in plots where the different species fell apart. Also the variables (measurements) were plotted against each other, in order to recognize the variables that were chiefly responsible for separating the different species.

## Results

A. All species

In the first PCA (Fig. $3 \mathrm{a}-\mathrm{c}$ ), all nine species were included. The first projection ( $\mathrm{X}=\mathrm{PC} 1, \mathrm{Y}=\mathrm{PC} 2$ ) clearly showed that $S$. alpinus was distinctly separated from all other species. It also showed a division of the remaining species into two groups, one containing S. araneus, S. coronatus, S. granarius, S. isodon and S. samniticus and the other consisting of $S$. caecutiens, S. minutissimus and S. minutus. In this latter group $S$. minutissimus was clearly separated from the other two species. $53.1 \%$ of the variance was explained by this component. The second projection ( $\mathrm{X}=\mathrm{PC} 1$, $\mathrm{Y}=$ PC 3) which explained $8.9 \%$ of the total variance confirmed the separation of S. caecutiens, S. minutissimus and S. minutus from the other species (however, without setting $S$. minutissimus apart from the other two species) and finally the projection of the second and third component $(\mathrm{X}=\mathrm{PC} 2, \mathrm{Y}=\mathrm{PC} 3)$ confirmed the separation of S. alpinus from all other species, and explained $6.05 \%$ of the total variance. In both these two latter projections there were some outliers of S. araneus. Together the three projections explained $68.0 \%$ of the variance. A variable loading


Fig. 3: Plots $1-3.3 \mathrm{a}-\mathrm{c}$ shows plot $1,3 \mathrm{~d}$ shows plot 2 (first projection only), $3 \mathrm{e}-\mathrm{f}$ shows plot 3, first (3e) and third (3f) projections. A $=$ S. alpinus, $\mathrm{C}=$ S. coronatus, $\mathrm{G}=$ S. granarius, $\mathrm{I}=S$. isodon, $\mathrm{K}=S$. caecutiens, $\mathrm{L}=S$. minutus, $\mathrm{M}=$ more than one individual (or for the variable plots, more than one variable) in the same spot, $\mathrm{R}=S$. samniticus, $\mathrm{S}=\mathrm{S}$. araneus, $\mathrm{V}=$ S. minutissimus.
plot of the same material showed that the most important factors separating $S$. alpinus from all other species were a longer $\mathrm{A}^{5}$, lacrimal foramen placed further back, a twocusped $\mathrm{A}_{1}$ and mental foramen placed more anteriorly.

The separation of the remaining species into two groups were purely metric, the "caecutiens-minutissimus-minutus-group" included smaller animals than the other group. The separation of S. minutissimus from S. caecutiens-minutus was chiefly due to even smaller overall measurements and to the mental foramen positioned further back.

## B. Sorex caecutiens and S. minutus

The second PCA plot (Fig. 3d) showed the two remaining species of the smaller group, S. caecutiens and $S$. minutus. At least the two first projections showed a gradual separation of the two species.

The first component explained $38.1 \%$ of the variance, the other two did not contribute much, $4.8 \%$ and $4.1 \%$ of the total variance respectively, the total variance explained was $47 \%$. A discriminant PLS analysis applicated on these two species showed a clearly significant class separation according to cross validation ( $37.9 \%$ of the variance explained by the first latent variable and $3.5 \%$ by the second, a total of $41.5 \%$ ). The characters most important in separating the species were that $S$. minutus had larger medial tines, lacrimal foramen placed further back, mental foramen positioned more in front and smaller overall measurements than in $S$. caecutiens.

## C. The remaining species

The third PCA plot (Fig. 3e-f) contained the five remaining forms, S. araneus, $S$. coronatus, S. granarius, S. isodon and S. samniticus. Four of them are very similar morphologically, while $S$. isodon is clearly distinguishable. It was somewhat surprising to find this species grouped together with the other four. The first component (Fig. 3e) explained $18.1 \%$ of the variance and was clearly grouping the animals in size. The second component explained $14.8 \%$ of the total variance, and here $S$. isodon tended to drift apart. The third component (Fig. 3 f ) finally set $S$. isodon very clearly apart from the other species, explaining $7.9 \%$ of the total variance, the total variance explained was $40.7 \%$. Discriminant PLS analyses between S. isodon and each of the four remaining forms did, however, not show any greater significance than discriminant PLS between these other species, the variance explained was $30.8 \%$ for $S$. isodon - S. araneus, $29.8 \%$ for $S$. isodon - S. coronatus, $40.1 \%$ for S. isodon - S. granarius and $30.8 \%$ for $S$. isodon - S. samniticus while the variance explained by PLS between the other four species was between $22.8 \%$ and $37.2 \%$ (see below).

Variables separating $S$. isodon from the other four species (see variable plot, Fig. 4a) were: 1. Longer antemolar toothrow in upper jaw; 2. Distinctly larger $A^{5}$; 3. Lesser width of $\mathrm{P}^{4}$ and $\mathrm{M}^{1}$; 4. Lacrimal foramen placed further back; 5. Unpigmented hypocones on upper molars (separates only against $S$. araneus and $S$. coronatus); 6. Mental foramen placed in more frontal position.


Fig. 4: 4a) A variable plot corresponding to Fig. 3 e. 4 b) plot 4 (first projection). 4c) plot 5 (first projection). $4 \mathrm{~d}-\mathrm{f}$ ) PLS-plots for S. araneus - S. coronatus (4d), S. araneus - S. granarius (4e) and S. coronatus - S. granarius (4f).

Table 2: Mean values and standard deviation (s) of measurements taken in mm (see Material and methods). Only the continuous metrical measurements are included in this table, and for those taken both on left and right side, only those taken on the left are given. Readers interested in the remaining values can obtain these from the author. A $=$ S. alpinus, $\mathrm{B}=$ S. araneus, $\mathrm{C}=S$. caecutiens, $\mathrm{D}=$ S. coronatus, $\mathrm{E}=S$. granarius, $\mathrm{F}=S$. isodon, $\mathrm{G}=$ S. minutissimus, $\mathrm{H}=S$. minutus, $\mathrm{I}=S$. samniticus.

|  | A | B | C | D | E | F | G | H | I |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 17.704 | 17.046 | 15.274 | 17.263 | 15.836 | 17.768 | 11.852 | 14.060 | 16.581 |
| s | 0.451 | 0.635 | 0.554 | 0.480 | 0.493 | 0.603 | 0.526 | 0.726 | 0.476 |
| 2 | 1.138 | 1.387 | 1.116 | 1.496 | 1.316 | 1.254 | 0.900 | 0.963 | 1.270 |
| s | 0.140 | 0.140 | 0.146 | 0.122 | 0.151 | 0.189 | 0.076 | 0.090 | 0.101 |
| 3 | 4.833 | 4.539 | 3.800 | 4.903 | 4.621 | 4.782 | 3.629 | 3.490 | 4.926 |
| s | 0.159 | 0.360 | 0.189 | 0.189 | 0.185 | 0.308 | 0.154 | 0.179 | 0.146 |
| 4 | 3.943 | 3.397 | 2.964 | 3.466 | 3.516 | 3.665 | 2.550 | 2.660 | 3.513 |
| s | 0.130 | 0.238 | 0.142 | 0.150 | 0.121 | 0.228 | 0.079 | 0.109 | 0.066 |
| 6 | 5.583 | 5.553 | 5.077 | 5.441 | 5.185 | 6.130 | 3.409 | 4.400 | 4.999 |
| s | 0.243 | 0.304 | 0.314 | 0.240 | 0.162 | 0.604 | 0.280 | 0.348 | 0.241 |
| 7 | 1.513 | 1.812 | 1.542 | 1.803 | 1.580 | 1.630 | 1.299 | 1.175 | 1.746 |
| s | 0.073 | 0.125 | 0.079 | 0.139 | 0.130 | 0.158 | 0.082 | 0.075 | 0.133 |
| 8 | 1.095 | 1.352 | 1.130 | 1.293 | 1.175 | 1.253 | 0.961 | 0.883 | 1.169 |
| s | 0.071 | 0.139 | 0.063 | 0.144 | 0.094 | 0.110 | 0.075 | 0.072 | 0.069 |
| 9 | 2.805 | 2.444 | 2.127 | 2.336 | 2.013 | 2.561 | 1.325 | 1.834 | 2.111 |
| s | 0.113 | 0.115 | 0.122 | 0.149 | 0.068 | 0.151 | 0.085 | 0.129 | 0.096 |
| 10 | 4.369 | 4.075 | 3.400 | 4.087 | 3.980 | 4.086 | 3.041 | 3.149 | 4.400 |
| s | 0.119 | 0.270 | 0.187 | 0.137 | 0.166 | 0.146 | 0.088 | 0.225 | 0.177 |
| 11 | 0.821 | 0.810 | 0.720 | 0.805 | 0.678 | 0.778 | 0.516 | 0.557 | 0.689 |
| s | 0.054 | 0.062 | 0.085 | 0.044 | 0.067 | 0.094 | 0.065 | 0.053 | 0.079 |
| 12 | 0.730 | 0.794 | 0.608 | 0.771 | 0.632 | 0.656 | 0.418 | 0.502 | 0.673 |
| s | 0.048 | 0.065 | 0.067 | 0.054 | 0.051 | 0.093 | 0.020 | 0.044 | 0.067 |
| 13 | 0.665 | 0.646 | 0.536 | 0.577 | 0.499 | 0.596 | 0.384 | 0.504 | 0.477 |
| s | 0.043 | 0.064 | 0.051 | 0.051 | 0.049 | 0.061 | 0.044 | 0.050 | 0.036 |
| 14 | 0.572 | 0.524 | 0.444 | 0.447 | 0.401 | 0.500 | 0.306 | 0.408 | 0.367 |
| s | 0.048 | 0.052 | 0.050 | 0.044 | 0.042 | 0.067 | 0.028 | 0.048 | 0.061 |
| 15 | 0.465 | 0.300 | 0.264 | 0.242 | 0.250 | 0.365 | 0.184 | 0.262 | 0.305 |
| s | 0.054 | 0.051 | 0.034 | 0.044 | 0.028 | 0.050 | 0.024 | 0.043 | 0.038 |
| 16 | 1.209 | 1.402 | 1.195 | 1.464 | 1.496 | 1.369 | 1.035 | 0.924 | 1.327 |
| s | 0.089 | 0.159 | 0.113 | 0.151 | 0.100 | 0.217 | 0.116 | 0.134 | 0.126 |
| 29 | 9.032 | 8.498 | 7.791 | 8.853 | 8.435 | 9.307 | 5.978 | 6.935 | 8.625 |
| s | 0.197 | 0.464 | 0.454 | 0.240 | 0.253 | 0.427 | 0.113 | 0.283 | 0.136 |
| 30 | 4.686 | 4.456 | 3.659 | 4.760 | 4.602 | 4.618 | 3.529 | 3.374 | 4.963 |
| s | 0.149 | 0.335 | 0.108 | 0.147 | 0.126 | 0.230 | 0.076 | 0.162 | 0.161 |
| 31 | 7.780 | 7.183 | 6.393 | 7.582 | 6.972 | 7.791 | 4.951 | 5.755 | 7.404 |
| s | 0.221 | 0.271 | 0.242 | 0.288 | 0.268 | 0.306 | 0.170 | 0.249 | 0.164 |
| 32 | 5.074 | 4.833 | 4.096 | 4.967 | 4.817 | 4.899 | 3.624 | 3.794 | 5.189 |
| s | 0.257 | 0.255 | 0.176 | 0.247 | 0.164 | 0.240 | 0.337 | 0.173 | 0.141 |
| 33 | 1.465 | 1.335 | 1.108 | 1.446 | 1.362 | 1.339 | 1.012 | 1.080 | 1.472 |
| s | 0.065 | 0.074 | 0.040 | 0.084 | 0.063 | 0.074 | 0.022 | 0.094 | 0.067 |
| 34 | 1.343 | 1.258 | 1.010 | 1.364 | 1.341 | 1.160 | 1.029 | 1.004 | 1.478 |
| s | 0.054 | 0.093 | 0.053 | 0.084 | 0.048 | 0.075 | 0.047 | 0.057 | 0.080 |


|  | A | B | C | D | E | F | G | H | I |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 35 | 1.259 | 1.220 | 1.081 | 1.312 | 1.194 | 1.272 | 1.003 | 0.972 | 1.355 |
| s | 0.051 | 0.081 | 0.038 | 0.069 | 0.075 | 0.076 | 0.046 | 0.068 | 0.044 |
| 36 | 1.319 | 1.279 | 1.020 | 1.376 | 1.326 | 1.160 | 1.056 | 0.990 | 1.480 |
| s | 0.063 | 0.071 | 0.057 | 0.081 | 0.044 | 0.057 | 0.068 | 0.057 | 0.064 |
| 37 | 1.154 | 1.025 | 0.936 | 1.050 | 1.056 | 1.105 | 0.876 | 0.853 | 1.161 |
| s | 0.036 | 0.083 | 0.053 | 0.067 | 0.082 | 0.063 | 0.069 | 0.053 | 0.048 |
| 38 | 1.253 | 1.269 | 1.003 | 1.276 | 1.233 | 1.144 | 1.060 | 0.974 | 1.391 |
| s | 0.057 | 0.110 | 0.053 | 0.057 | 0.074 | 0.081 | 0.068 | 0.052 | 0.094 |
| 39 | 0.753 | 0.641 | 0.624 | 0.755 | 0.714 | 0.759 | 0.539 | 0.576 | 0.782 |
| s | 0.038 | 0.058 | 0.033 | 0.052 | 0.042 | 0.056 | 0.021 | 0.038 | 0.063 |
| 40 | 1.155 | 1.278 | 0.978 | 1.141 | 1.100 | 1.158 | 0.963 | 0.935 | 1.185 |
| s | 0.046 | 0.127 | 0.045 | 0.081 | 0.056 | 0.091 | 0.060 | 0.058 | 0.084 |
| 61 | 8.998 | 7.715 | 6.672 | 8.166 | 7.945 | 8.414 | 5.394 | 6.078 | 8.305 |
| s | 0.412 | 0.312 | 0.262 | 0.241 | 0.297 | 0.338 | 0.144 | 0.224 | 0.311 |
| 62 | 3.706 | 4.038 | 3.186 | 4.211 | 3.758 | 4.273 | 2.748 | 2.691 | 4.105 |
| s | 0.132 | 0.145 | 0.119 | 0.125 | 0.184 | 0.184 | 0.071 | 0.187 | 0.107 |
| 63 | 2.520 | 2.700 | 2.290 | 3.023 | 2.616 | 2.935 | 2.066 | 2.042 | 2.822 |
| s | 0.145 | 0.191 | 0.123 | 0.168 | 0.205 | 0.167 | 0.031 | 0.117 | 0.101 |
| 64 | 3.196 | 3.448 | 3.145 | 3.584 | 3.118 | 3.431 | 2.307 | 2.501 | 3.380 |
| s | 0.136 | 0.193 | 0.123 | 0.135 | 0.183 | 0.169 | 0.089 | 0.171 | 0.072 |
| 66 | 5.166 | 4.705 | 4.005 | 4.736 | 4.377 | 4.995 | 3.323 | 3.680 | 4.766 |
| s | 0.207 | 0.220 | 0.131 | 0.128 | 0.114 | 0.204 | 0.129 | 0.213 | 0.179 |
| 67 | 1.077 | 0.947 | 0.794 | 0.902 | 0.810 | 1.012 | 0.550 | 0.706 | 0.861 |
| s | 0.038 | 0.079 | 0.072 | 0.066 | 0.067 | 0.093 | 0.029 | 0.092 | 0.088 |
| 69 | 0.997 | 1.059 | 0.917 | 1.049 | 0.987 | 1.120 | 0.779 | 0.828 | 1.056 |
| s | 0.091 | 0.075 | 0.046 | 0.069 | 0.093 | 0.083 | 0.042 | 0.060 | 0.084 |
| 71 | 1.344 | 1.831 | 1.244 | 1.473 | 1.226 | 1.555 | 0.980 | 1.061 | 1.380 |
| s | 0.146 | 0.152 | 0.185 | 0.199 | 0.141 | 0.178 | 0.066 | 0.167 | 0.170 |
| 72 | 0.997 | 0.984 | 0.751 | 1.066 | 0.935 | 0.994 | 0.540 | 0.711 | 1.006 |
| s | 0.091 | 0.103 | 0.066 | 0.070 | 0.063 | 0.065 | 0.061 | 0.080 | 0.083 |
| 73 | 1.386 | 1.339 | 1.162 | 1.359 | 1.284 | 1.397 | 0.991 | 1.047 | 1.355 |
| s | 0.052 | 0.071 | 0.041 | 0.059 | 0.054 | 0.059 | 0.047 | 0.050 | 0.069 |
| 74 | 0.820 | 0.832 | 0.623 | 0.842 | 0.824 | 0.863 | 0.635 | 0.568 | 0.916 |
| s | 0.044 | 0.057 | 0.041 | 0.054 | 0.069 | 0.066 | 0.034 | 0.039 | 0.057 |
| 75 | 0.904 | 0.885 | 0.647 | 0.894 | 0.869 | 0.880 | 0.630 | 0.630 | 0.971 |
| s | 0.054 | 0.058 | 0.040 | 0.049 | 0.061 | 0.054 | 0.033 | 0.039 | 0.051 |
| 76 | 1.156 | 1.086 | 0.954 | 1.151 | 1.058 | 1.132 | 0.898 | 0.904 | 1.171 |
| s | 0.040 | 0.061 | 0.025 | 0.050 | 0.048 | 0.040 | 0.039 | 0.044 | 0.046 |
| 77 | 0.814 | 0.798 | 0.593 | 0.815 | 0.810 | 0.821 | 0.635 | 0.574 | 0.916 |
| s | 0.047 | 0.059 | 0.046 | 0.051 | 0.065 | 0.067 | 0.037 | 0.034 | 0.062 |
| 78 | 0.863 | 0.819 | 0.609 | 0.811 | 0.820 | 0.844 | 0.631 | 0.603 | 0.898 |
| s | 0.048 | 0.052 | 0.052 | 0.053 | 0.062 | 0.064 | 0.054 | 0.040 | 0.056 |
| 79 | 0.968 | 0.928 | 0.840 | 0.940 | 0.881 | 0.938 | 0.775 | 0.793 | 0.987 |
| s | 0.046 | 0.061 | 0.038 | 0.040 | 0.047 | 0.049 | 0.060 | 0.044 | 0.054 |
| 80 | 0.705 | 0.653 | 0.504 | 0.662 | 0.681 | 0.681 | 0.507 | 0.497 | 0.754 |
| s | 0.029 | 0.038 | 0.040 | 0.048 | 0.062 | 0.045 | 0.023 | 0.042 | 0.059 |
| 81 | 0.597 | 0.586 | 0.428 | 0.526 | 0.526 | 0.580 | 0.377 | 0.421 | 0.580 |
| s | 0.035 | 0.061 | 0.040 | 0.063 | 0.050 | 0.053 | 0.042 | 0.037 | 0.049 |


|  | A | B | C | D | E | F | G | H | I |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 82 | 0.785 | 0.787 | 0.613 | 0.813 | 0.799 | 0.790 | 0.533 | 0.539 | 0.810 |
| s | 0.065 | 0.097 | 0.055 | 0.072 | 0.061 | 0.064 | 0.063 | 0.072 | 0.070 |
| 83 | 0.303 | 0.315 | 0.266 | 0.350 | 0.320 | 0.303 | 0.225 | 0.238 | 0.338 |
| s | 0.036 | 0.040 | 0.030 | 0.054 | 0.023 | 0.042 | 0.043 | 0.048 | 0.027 |
| 85 | 1.880 | 1.554 | 1.405 | 1.715 | 1.579 | 1.585 | 1.092 | 1.210 | 1.559 |
| s | 0.112 | 0.127 | 0.102 | 0.137 | 0.132 | 0.149 | 0.056 | 0.108 | 0.101 |
| 86 | 2.026 | 1.763 | 1.526 | 1.989 | 1.810 | 1.824 | 1.284 | 1.335 | 1.815 |
| s | 0.115 | 0.130 | 0.066 | 0.147 | 0.097 | 0.141 | 0.064 | 0.098 | 0.090 |
| 87 | 0.562 | 0.678 | 0.508 | 0.659 | 0.650 | 0.702 | 0.515 | 0.457 | 0.686 |
| s | 0.042 | 0.064 | 0.048 | 0.053 | 0.060 | 0.087 | 0.040 | 0.038 | 0.058 |
| 88 | 1.125 | 1.130 | 0.906 | 1.154 | 1.061 | 1.122 | 0.885 | 0.771 | 1.157 |
| s | 0.054 | 0.092 | 0.058 | 0.065 | 0.063 | 0.093 | 0.060 | 0.064 | 0.060 |
| 89 | 0.417 | 0.389 | 0.315 | 0.423 | 0.426 | 0.360 | 0.304 | 0.287 | 0.417 |
| s | 0.043 | 0.037 | 0.035 | 0.043 | 0.038 | 0.046 | 0.043 | 0.035 | 0.036 |

## D. S. araneus, S. coronatus, S. granarius and S. samniticus

After the first three PCAs all species are separated except the four morphologically very similar species treated by Hausser (1984). A PCA was made on all four species (Fig. 4b), another one on the three members of the S. araneus/arcticus-group (Fig. 4 c ), and finally discriminant PLS analyses were made between all the species, two and two at a time (Fig. $4 \mathrm{~d}-\mathrm{f}$ ). The PCA on all four species showed rather good separation of all four species in the first component (Fig. 4b) (which explained $20.9 \%$ of the variance), clear separation of $S$. coronatus in the second component (explaining $16.5 \%$ ) and separation of $S$. araneus and $S$. coronatus but not of the other two species in the third (explaining $5.9 \%$ ); the total variance explained was 43.3 \%.

The PCA on S. araneus, S. coronatus and S. granarius showed good separation of all three species in the first (Fig. 4c) and third components, less so in the second. The components explained respectively $22.1 \%, 13.3 \%$ and $5.0 \%$ of the variance, a total of $40.4 \%$. In this PCA some strong outliers occurred, one very strong outlier of $S$. araneus in the second and third projections was due to a measuring fault, but another $S$. araneus was separated among the $S$. coronatus in the third projection. This individual had a greater width and length of $\mathrm{M}^{1}$ than other skulls of the same species (the differences were, however, very slight). Finally one S. coronatus was separated very ciearly among the $S$. araneus in the first and third projections, due to a longer total length of the upper antemolars and larger height of the internal temporal fossa. In this last case the possibility of misidentification of the skull cannot be excluded.

Discriminant PLS analyses applicated on the different species, two and two at a time, showed good separation of all the species. The variance explained was $27.3 \%$ for $S$. araneus $-S$. coronatus (Fig. 4 d ), $34.5 \%$ for $S$. araneus $-S$. granarius (Fig.

4 e ), $35.7 \%$ for $S$. coronatus $-S$. granarius (Fig. 4 f ), $37.2 \%$ for $S$. araneus $-S$. samniticus, $22.8 \%$ for $S$. coronatus - S. samniticus and $35.7 \%$ for S. granarius S. samniticus.

A discriminant PLS applicated on all four species simultaneously showed, however, nothing not already present in the PCAs, it explained a total of $43 \%$ of the variance.

The characters separating the four species were mostly metric and in almost all cases the measurements were overlapping, which made identification in this group very difficult. S. samniticus has, however, a few distinct characters such as the shape of the upper incisor (Graf et al. 1979; this character was not included in the present measuring program) and the position of medial tines on the same tooth (Dannelid 1989). Also one difference that seemed fairly constant was that $S$. samniticus showed greater width over the trigonids on the lower molars than the other species. Apart from that all of these species were very similar. Statements on size differences refer to the mean values.

Characters separating S. araneus from:
a) S. coronatus: Condylobasal length shorter, upper antemolar toothrow longer, width and length of $\mathrm{M}^{1}$ smaller. Mandible shorter and width and length of $\mathrm{M}_{3}$ smaller, height of internal temporal fossa larger.
b) S. granarius: Overall larger measurements, especially the condylobasal length and the upper antemolar toothrow, lacrimal foramen placed a little more anteriorly.
c) S. samniticus: Condylobasal length larger, palatal length shorter, glenoid width shorter, width of molars (especially trigonid width of lower molars) smaller.

Characters separating S. coronatus from:
a) S. granarius: The same as those separating S. araneus from S. granarius.
b) S. samniticus: Condylobasal length larger, trigonid width of lower molars smaller.

Characters separating S. granarius from S. samniticus: Coronoid process lower, trigonid width of lower molars much smaller (overlapping very little).

Also by using several metric characters like condylobasal length, length of upper antemolar toothrow and length of first upper antemolar it was possible to build two groups, one consisting of larger forms (S. araneus and S. coronatus) and one consisting of smaller forms (S. granarius and S. samniticus). However, S. coronatus and S. samniticus had a greater palatal length than S. araneus and S. granarius. S. samniticus showed greater width between the $\mathrm{M}^{2}$ than the other species. $S$. araneus clearly showed a greather height of the internal temporal fossa than the remaining species. S. granarius showed lesser height of the coronoid process than the other three species.

The characters mentioned are not all separating the different species but are those which, from the variable plots, appear to be most important. It must be remembered that since almost all measurements overlap it is a combination of characters, not the characters themselves, that separates the species. Hausser \& Jammot (1974) found four characters by which it was possible to make a $95,3 \%$ discrimination between S. araneus and S. coronatus, none of these characters was, however, included in the present study.

## Discussion

The plots made a clear distinction between most of the Sorex-species analysed in this work. This is not, however, necessarily a phylogenetic distinction. It must be remembered that statistical methods applied on pure skull morphology may sometimes more reflect the overall similarity rather than the phylogeny, since it is hard to detect convergences and parallel evolutions with these methods. For example S. caecutiens, $S$. minutissimus and $S$. minutus were discriminated against the other species chiefly because of their smaller size. Increase and decrease in size, however, might have occurred many times in different Sorex-lineages.

If the plots should give good information they have to be compared with karyological and electrophoretical data. S. alpinus was the most isolated species according to the plots, and this is also the case according to electrophoresis (Catzeflis et al. 1982) and probably also to the karyotype (Meylan 1964). Apparently this species has got no close relatives in Europe (and probably nowhere else), it must be regarded as an old relic species.

In the case of $S$. alpinus all data point in one direction; this is, however, not the case with the second group separated in the plots, the smaller species $S$. caecutiens, S. minutissimus and S. minutus. They are separated chiefly because they are smaller; but within the group considerable size differences are present. Karyologically all belong to a "group" characterized by a chromosomal number of 42 or close to 42 , but this group might not be a natural one. Electrophoretical results indicate that the three small species do not form a phylogenetic group (Catzeflis 1984, in his work $S$. minutissimus was not included). They are probably species with plesiomorphous chromosome characters (they lack the sex chromosome specialisations of the $S$. araneus/arcticus-group), but this also applies to $S$. isodon and $S$. samniticus.

Of the five remaining species, $S$. isodon was clearly separated from the others in the plots. Karyologically, $S$. isodon is most similar to $S$. caecutiens. It might well be argued that $S$. isodon and $S$. caecutiens are related and that the plot discriminance between them is due chiefly to size differences.

The four remaining species make up the troublesome part. They are all very similar morphologically and it is only possible to separate them chiefly by using a combination of characters. However, chromosomes and electrophoresis give another view: $S$. araneus, S. coronatus and S. granarius are closely related while $S$. samniticus remains very much apart. Hausser (1984) made statistical analyses of these four species using SPSS, using not only principal component and discriminant analyses as in this work, but also multiple regression and canonical correlation analyses. He also included geoclimatic variables which is outside the scope of this work. He stated convincingly that the morphological differences between the four species could be partly explained by habitat conditions but not by ecological shifts into new niches. His conclusion was that the "araneus"-niche was a highly successful one that allowed animals to exist for a long time morphologically unchanged. S. samniticus might thus be a remnant of earlier Sorex-occupants of this niche, or it might (less likely) be the result of an isolated Italian speciation into that niche.

A comparison between the karyological data, the electrophoretical data and the morphological data (as expressed in these plots) indicates that the phylogeny is more
consistently reflected in the karyological and electrophoretical data, while the morphological data reflects both phylogenetic and ecological differences. In some cases (the position of S. alpinus and the close relationship of $S$. araneus $-S$. coronatus - S. granarius) the morphological results are in accordance with results achieved by cytological research and electrophoresis, in other cases not. In these cases the author suggests that similarities and differences in gross morphology should be regarded as the result of ecological adaptations.

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## Zusammenfassung

Schädel von 9 Arten von Spitzmäusen der Gattung Sorex wurden mit Hilfe eines BildAnalysators gemessen. Von jedem Schädel wurden 120 Messungen genommen. Diese wurden dann statistisch verarbeitet unter Verwendung multivariabler Analysenprogramme (SIMCApackage). Die Resultate zeigten deutliche Unterschiede zwischen allen Arten. Die morphologischen Ergebnisse werden mit Chromosomendaten und Elektrophoresebefunden verglichen und es wird diskutiert, inwieweit Unterschiede die Phylogenie widerspiegeln oder als Resultat ökologischer Anpassungsprozesse verstanden werden müssen.

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[^0]:    ${ }^{*}$ ) Note added in proof $=$ S. causasicus should, according to Zaitsev, Zool. Zh. 67: 1878-1888, 1988, be called S. satunini.

